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POPULATION DYNAMICS OF THE MOUNTAIN PINE BEETLE IN LODGEPOLE PINE

PROGRESS REPORT 1961 - 1962

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CONTENTS

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SUMMARY

1. Statistical distributions for attack and gallery densities appear to be normal but contagious for brood densities.

2. The breast height is the most consistent sample location for the late larval and pupal beetle populations.

3. Sample sizes needed at a prescribed level of accuracy are shown in the text.

4. Attack, gallery and brood density, based on a square foot unit, increase in density with the increase in tree diameter.

5. A sampling scheme that approaches randomization is presented in the text.

6. Parasite-predator distribution within and between trees appeared to follow bark thickness rather than brood density.

7. Simplified life tables are presented for the two populations studied.

GENERAL

The study of population dynamics of the mountain pine beetle in lodgepole pine began in the fall of 1961. This progress report covers the beetle attack period, fall 1961, through the beetle emergence period, summer 1962, or one generation.

OBJECTIVES

Three main areas of research in short-term studies in a study plan of April 1962 are:

1. Development of sampling precedures.

   a. Determine sample sizes, sampling frequency, sample location, and methods to measure populations of the host insect and its parasites and predators.

b. Develop methods to determine significance of stand characteristics such as stand composition, diameter classes, site quality, age classes, soil moisture, rate of growth, etc., within infestations.

2. Studies of populations.

   a. Determine characteristics of beetle broods at varying population levels.

   b. Determine effects of seasonal weather conditions on population development--temperature, humidity, rainfall, snow depth, etc., and duration of each.

3. Studies of infestations.

   a. Study tree and stand characteristics in areas with histories of epidemic, static, endemic, and no infestations.

Due to lack of adequate manpower, not all of the studies were started, nor was it possible to attain our objectives in those started. Study 1b was deleted and studies 2b and 3a merely approached in a subjective manner. Actually, studies 1a and 3a would require full time of at least one man.

METHODS

During the year of the study, study 1a dealt with the sample size and location and included the following size comparisons:

1. One-tenth square foot circular sample vs. one-tenth square foot square sample.

2. One-fourth square foot circular sample vs. one-fourth square foot square (6"x6") sample.

3. One-fourth square foot rectangular (6"x6") sample vs. one-half square foot rectangular (6"x12") sample vs. one-fourth of the circumference of the tree by 12 inches in length sample.

These samples were taken at the following locations on the tree:

1. At breast height on the north and south sides of the tree.
2. At 5 feet below the height of attack on the north and south sides of the tree.
3. At a location midway between the above 2 samples.

Ten trees were sampled according to the scheme within each of four diameter classes: 6-9, 9-12, 12-15 inches, and greater than 15 inches d.b.h. Samples were superimposed on one another in a nested fashion. The two areas of infestation sampled were on the Wasatch and the Teton National Forests.

As planned, both attack and brood data were to be obtained from these samples and repeated at least three times during the generation year. Because of a late start in the field and the laborious and time-consuming nature of the sampling, the plans had to be changed. Brood data was limited to the rectangular samples on 13 trees. Data on attack density and inches of gallery were taken from all sample sizes, shapes, and from all 40 trees.

An arch punch (Furniss 1962) was used for taking each circular sample and a 2-inch square punch constructed for the rectangular samples. All three sizes of punches served only to delineate the sample area because lodgepole pine bark cannot usually be easily removed from the tree.

The field phase of study 2a to determine characteristics of beetle broods at varying population levels utilized the 1/4 circumference by 12 inches long sample size as a starting point. This sample size served in two ways: (1) caged area, and (2) bark sample area. The caged samples were placed on the north side of the tree and an equal size bark sample removed from the east side of the tree. The sample locations on the tree's stem and the diameter classes sampled were the same as described above.

The two types of sampling areas were undertaken at two-week intervals except during winter months. This resulted in seven sets of samples, one tree in each diameter class from each of the two infestations.

The area to be caged was marked at the top and bottom by metal corugated fasteners (5/8 x 1 inch) driven through the bark to the xylem. This formed a barrier and prevented migration of larvae vertically. The cage was formed with a plastic screen stapled to the bark covering this area. The cage was funnel shaped at the bottom with a test tube inserted into the narrow neck and fastened with a rubber band. The test tube was crimped and a small hole made at the bottom for drainage. A circular plastic screen was placed in the bottom of the test tube, covered by an inch of paradichlorobenzene crystals and then a circular blotting paper placed on top of the crystals. The crystals killed the insects as they emerged and fell into the tube (fig. 1).

The bark sample was taken to show the relation of the population to the cage population at time of sampling. The cage sample allowed the brood to mature and emerge, thus showing brood reduction in sequence throughout the generation year.

Figure 1. Cage and bark sample used during 1962 study season.

The laboratory phase of study 2a dealt with intraspecific competition under controlled conditions. This work was previously reported (Cole 1962).

Work was begun on study 2b and, as it affects study 3a, weather records were taken to be compiled and evaluated as time allows. Hygrothermographs were set up at each study plot. Records were kept for the Wasatch plot during the growing season only, but for the entire year at the Teton plot. Maximum and minimum thermometers were set up for winter records on the Wasatch plot. These thermometers were read twice during the winter months. Data on precipitation, snow depth, and their duration were supplied by the Grand Teton National Park for the Teton plot.

RESULTS AND DISCUSSION

The results of the first year of study covering the development of a complete generation are discussed in brief. As is usual at the start of studies, early results are tentative. Considerable progress was made in reaching the objectives of our sampling schemes and ideas developed in other studies for further research.

The data from the sample size-location phase were thoroughly analyzed by Robert W. Carlson[1/], summer assistant. Only the results are discussed in this progress report. The type of statistical distributions were first sought for the three measurements: attack, gallery, and brood densities. Attach and gallery density appeared to be random or nearly normal. Brood density was not normal but of a contagious type of distribution. The variance of three measurements were subjected to a variance analysis. The table below summarizes the significant F ratios.

Source	Attacks	Gallery	Brood
Plot	*	*	-
Diameter	*	*	-
Sample size	*	*	N.S.
Aspect	-	-	*
Sample height	*	-	*
Plot by diameter		*	-
Plot by aspect	*	*	*
Diameter by height	*	-	-
Aspect by height	-	-	*

1/ The complete analysis and details are presented in Carlson's thesis as partial fulfillment for the requirements of a degree of Master of Science, Department of Natural Resources, University of Michigan, Ann Arbor.

Sample sizes needed at a prescribed level of accuracy were calculated and shown below as they appear in the thesis.

Table 1.--The number of trees required to be sampled for a 20 percent SME at 2/3 probability based upon non-summed north and south bottom samples (rectangular samples only)

	Plot	Sample size 1/10	1/4	1/2	1/4-Circum.
		Square feet			
Attack density	Teton	6.53	2.48	1.78	1.10
	Wasatch	4.81	2.75	1.91	1.54
Gallery density	Teton	2.56	2.26	2.14	1.86
	Wasatch	1.89	1.45	1.14	0.95
Brood density	Teton	7.19	6.78	5.72	5.36
	Wasatch	42.50	44.57	48.05	38.38

Table 2.--The number of trees required to be sampled for a 20 percent SME at 2/3 probability based upon summed north and south bottom samples (rectangular samples only)

	Plot	Sample size 1/10	1/4	1/2	1/4-Circum.
		Square feet			
Attack density	Teton	9.13	3.36	2.42	3.13
	Wasatch	7.76	4.22	3.63	3.08
Gallery density	Teton	6.40	5.71	5.56	4.67
	Wasatch	2.46	2.63	2.20	2.12
Brood density	Teton	8.19	9.93	8.16	7.56
	Wasatch	54.06	66.94	67.84	55.36

In general, the sample at breast height is most consistent. Randomization is needed to sample aspect correctly. As previously discovered the attack and gallery density is related and both will increase in density with the increase in diameter.

Carlson (1963) presents a sampling scheme that approaches randomization, and which is worth considering for the coming season. Sample size would be the 1/10-square-foot rectangle (3.6 x 4 inches). The

area on the infested tree to be randomly sampled would be a zone 1 foot above and 1 foot below breast height. The sample zone is divided into four cardinal quadrants and six levels of 4 inches each, three above and three below breast height; thus, 24 possible samples. The selection for locating two samples per tree can be done prior to the field season and by random numbers. The chance of the second sample being the same as the first sample location is 1 in 552. Sample selection is without replacement of the number drawn.

The analysis of data from the cage technique for population studies (study 2a) was limited to the analysis of variance to show differences between factors measured. The factors involved were: (1) attack density from which the attacking population was calculated, (2) inches per attack, (3) emerging population, and (4) the parasite-predator complex as an entity and as species. All data were converted to a square foot basis.

The bark-cage technique did not prove successful. This technique was used in the hope that by sampling the population at the time of caging a relationship might exist between the brood counted (bark) and the population that emerged (cage). In addition to trapping the emerging population, the cage served to exclude successive brood reduction caused by parasites and predators, and to establish the time and identity of the factors of reduction present at the time of caging. Evidently, the majority of the parasites and predators were present at the first caging as this technique showed no difference in the emerging host population between the time of first and last cagings.

Brood density.--The bark sampling did reveal rather interesting population decreases (and increases) between time of sampling and infestations.

The following tables show the results of the brood sampling at intervals during life cycle:

Table 3.--Progressive mean brood reduction (or increase) during life cycle

Area	Cage position	Parent adult	Sampling intervals 1	2	3	4	5	6	7	Emerging adults
Wasatch	H	16.8	-	-	172.7 1/	58.9	35.5	0	6.0	2.3
	L	22.4	-	-	206.6 1/	104.6	31.1	10.0	8.3	1.6
Teton	H	16.0	-	113.2 2/	84.5	14.8	28.5	83.4	56.0	50.7
	L	17.2	-	218.1 2/	59.7	39.6	11.1	43.6	153.7	53.2

Table 4.--Percent decrease or increase during life cycle

Area	Cage position	Sampling intervals 1	2	3	4	5	6	7	Total brood reduction	Parent adults to new adults
Wasatch	H	-	-	0 1/	65.9	39.7	-	83.1	96.5	98.7
	L	-	-	0 1/	49.4	70.3	67.9	17.0	96.0	99.3
Teton	H	-	0 2/	25.4	82.5	89.2+	192.6+	32.9	50.5	216.9+
	L	-	0 2/	72.6	33.7	72.0	292.8+	252.5+	32.9	209.3+

1/ Average of first three observations

2/ Average of first two ovservations

Had the Teton brood followed the reduction pattern of the Wasatch brood, the emerging adults for that plot would have been 1.5 and 1.6 respectively for the high and low cages. Evidently the Teton parent adults resumed egg laying in the spring (sampling interval 5) as is later brought out in the section "inches per attack", and table 11, thus possibly accounting for the increase in population.

Attack density.--Four main sources of variation were used: two infestations, two sides of tree attacked, four diameters at breast height, and two heights of sample. Only the side of tree attacked showed no significant difference between the attack densities. The Wasatch plot, as expected, had the greater attack density at the lower cage position. The attack density increased by diameter classes. Infestation by height was the only significant interaction. This variation was probably due almost entirely to the Wasatch low cage. The following table shows the means for these sources of variation:

Table 5.--Means of sources of variation of variates

Source of variance	Means of variates			
Infestation	Wasatch 9.37			Teton 7.88
Side of tree	East 8.98			North 8.26
Height of sample	High 7.43			Low 9.82
Diameter class	< 9	9-12	12-15	> 15
	6.26	7.18	9.59	11.46
Infestation x height	Wasatch			Teton
	High 7.69			7.16
	Low 11.05			8.59

Inches per attack.--The same sources of variation were used here as with attack density. In this case, sampling height was the only source that showed no difference in length of gallery per attack. Sampling height had no effect on the length of gallery. Even though the other sources of variation showed differences in length of gallery, the underlying main cause of difference was the dependence

of the length upon attack density. This fact had been brought out in the laboratory work (Cole 1962) and now was substantiated in the field. The table for the curvilinear regression calculated for attack density vs. inches per attack was as follows:

Attack/sq.ft.	Inches/attack
3	5.5
4-5	6.2 - 6.8
6-7	7.3 - 7.7
8-(10)-12	8.0-(90+)-8.0
13-14	7.6 - 7.2
15-16	6.7 - 6.0
17	5.3

Emergence of new adults.--The source of variation, side of tree sampled, was necessarily omitted in this analysis of variance since cages were placed only on the north side of the tree. In this case, height of sample was the only main source of variation showing no significant difference in the emergence. This fact can, in a sense, be considered in disagreement with the variation in attack density at these sampling heights. On the other hand, this fact points up that even though the attack density was greater at the lower sampling height, the emergence was equal between the two heights. Stated another way, there was actually greater survival of brood at the higher sampling height since there was less brood to begin with. This was true for both infestations since the interaction, area by height showed no significant difference.

By diameter class, the emergence, attack density (and parent adult density), and survival rate of the brood, acted in the same manner in both infestations. The larger the diameter the greater attack density (and parent adults); the greater the emergence; the less decrease in brood (Wasatch) or greater increase in brood (Teton) (table 7.)

Table 7.--Parent adults, fall brood, emerging adults and percent decrease/increase by diameter class by sample height by infestation per sq. ft.

Infes-tation	Height	State	≤ 9	9-12	12-15	≥ 15
Wasatch	High	Par. ad.	11.4	16.8	18.0	20.6
		Brood	128.0	163.0	219.1	163.3
		Em. ad.	0	0	2.8	6.2
		Percent	100(-)	100(-)	84.4(-)	69.9(-)
	Low	Par. ad.	12.1	23.6	29.2	29.4
		Brood	150.0	155.3	325.8	191.0
		Em. ad.	0	0.4	2.4	3.1
		Percent	100(-)	98.3(-)	91.8(-)	89.5(-)
Teton	High	Par. ad.	18.4	11.4	17.2	17.6
		Brood	57.0	35.0	156.6	203.9
		Em. ad.	1.2	32.9	52.5	102.1
		Percent	93.5(-)	186.6(+)	205.2(+)	480.1(+)
	Low	Par. ad.	12.8	14.1	19.4	21.2
		Brood	65.6	287.9	283.9	374.5
		Em. ad.	17.8	44.8	44.9	95.1
		Percent	39.1(+)	217.7(+)	131.4(+)	384.6(+)

Parasites-predators.--In this case, the source of variation, side of tree sampled, was also omitted due to the method of caging. Ten species of parasites, predators, and suspected agents of reduction were included in the analysis. The group of ten species showed no preference between diameter classes nor between heights of sampling when analyzed by combining the plots.

The group was more abundant on the Wasatch plot than on the Teton plot, and,as would be suspected, the abundance by species and species by infestation were significantly different. In fact, with further breakdown the differences were more apt to be shown. For example, the interactions: infestation by species, infestation by diameter, species by height, and infestation by species by height, were all significant at the 95 percent confidence level. Not only did the Wasatch plot have more parasites and predators but the order of abundance was not the same as on the Teton plot.

Table 8.--Parasite and predator abundance

Species (Per square foot)

Infestation	Sample height	*Entomobrya comparata*	*Coeloides dendroctoni*	Staphylinidae	*Epuraea linearis*	*Corticaria* sp.	Cleridae	Other Diptera	Other Hymenoptera	*Medetera* sp.
Wasatch	High	12.1	5.5	4.0	4.0	0.9	0.3	0.2	0.3	0.2
	Low	22.1	3.6	3.0	3.8	0.7	0.5	0.8	0.4	0.3
Teton	High	0.6	0.5	0.8	3.0	0.1	0.4	0.3	0.3	0.1
	Low	1.1	0.6	0.3	1.7	0.1	1.6	1.1	0.3	0.5

The decrease in adult beetle population for the < 9 d.b.h. class, low cage, and the least increase for the < 9 d.b.h. class, high cage, and the tremendous overall increase on the Teton plot can partially be explained in the following table showing the distribution of the parasite-preditor group:

Table 9.--Parasite and predator distribution per square foot, by plot, by diameter class

Infestation	Height	< 9	9-12	12-15	< 15
Wasatch	High	1.9	2.3	2.5	4.1
	Low	1.6	3.6	4.5	3.7
	High + Low	3.6	5.9	7.0	7.8
Teton	High	1.3	0.3	0.4	0.4
	Low	1.1	0.7	0.8	0.4
	High + Low	2.4	1.0	1.2	0.8

Even though the parasite-predator group was low in numbers on the Teton plot, the majority were in the smaller diameter trees--where the host population was the least. On the Wasatch plot the parasite-predator population proportionally followed the host population between the diameter classes. Bark thickness seemed to be the governing factor.

The following rudimentary life table was constructed to show the brood progression throughout the generation. One note of explanation is repeated here--the increase in brood within the Teton plot must have resulted from the resumption of egg laying by the female in the spring. The broods on the two study plots began, entered, and emerged from winter in close approximation of each other. Even the parasite-predator population decreases fairly uniformly in numbers from spring until emergence. Of course, sampling error could have produced the apparent increase in the Teton population. However, the uniform increase in both inches of egg gallery and brood population would indicate that sampling error was not responsible.

Table 10.--Rudimentary life table for the mountain pine beetle on the Wasatch and Teton plots for the generation 1961-1962.

x	l_x	d_xf	dx	
Sample period	No. alive at start of x (per sq. ft.)	Factors responsible for d_x and pct. of responsibility	No. dying during x (per sq.ft.)	100 qx d_x as pct. of l_x
		Wasatch		
0	19	(Parent adults)		
1	190	Competition, weather	108	57
2	82	Winter	49	60
3	33	Predators, competition	23	70
4	10	Predator, parasites and competition	3	30
5	7	Predator, parasites and competition	5	71
6	2	(New adults)		99
	(89% reduction from parent to new adults)			
		Teton		
0	16	(Parent adults)		
1	166	Competition, weather	93	56
2	73	Winter	45	62
3	28	Predators and competition	8	29
4	20	-	(+44)	+220
5	64	-	(+41)	+ 64
6	105	Predators, parasites and competition	53	51
7	52	(New adults)		69
	(+225% increase from parent to new adults)			

Table 11.--Inches of egg gallery, brood and predator-parasite populations at time of sampling (mean number per sq. ft.))

Sampling period	Inches gallery		Brood		Predator-parasite	
	Wasatch	Teton	Wasatch	Teton	Wasatch	Teton
1	8.7	7.0	190	166	47	9
2	4.4	7.0	82	73	37	9
			winter			
3	7.3	10.0	33	28	8	7
4	8.6	9,8	10	20	8	6
5	9.4	12.4	7	64	3	4
6	-	10.9	-	105	-	3

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